OBSERVATIONS ON THE TAXONOMY OF THE ANTS *MYRMICA RUBRA* L. AND *M. LAEVINODIS* NYLANDER. (HYMENOPTERA: FORMICIDAE.)

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With 3 Text-figures.

1. Distinction Between *Myrmica rubra* L. and *M. laevinodis* Nylander.

The species *Myrmica rubra* L. was divided by Nylander (1846) into three forms; of the two with curved scapes, one having workers with longer epinotal spines and a wrinkled area between was called *M. ruginodis*, and the other having smaller epinotal spines and a smooth area between was called *M. laevinodis* Nylander[1]. Numerous ants which would not fit into either type were classed as intermediates by Forel (1874) under the title *M. laevinodis* Nylander var. *ruginodo-laevinodis* Forel.

Nylander's distinction is satisfactory only if spine-length is assessed relative to head-width and a sample of the workers of a colony examined. These precautions are necessary for two reasons: first, because within each species colony mean spine-length increases with colony mean head-width, and *laevinodis* colonies of large workers[2] may have spines as long as *rubra* colonies of small workers. This means that by taking head-width into account in assessing spine-length, colonies which would have been classed as intermediate solely on a basis of spine-length fall definitely into one or other species group, being *laevinodis* if they have large heads, and *rubra* if they have small heads. The second precaution is necessary since individual workers from colonies of distinct species may be indistinguishable.

A sample of 25 workers was taken from each colony examined. Head-width was measured immediately behind the eyes, and spine-length as in fig. 1. When the average values of these for each nest were plotted graphically (fig. 2), they formed two distinct groups each showing internal regression of one character on the other. Details are set out in Table I.

Care has been taken to include in this survey specimens which Mr. Donisthorpe[3] considered typical and specimens which he said would fall into Forel's intermediate category. After measurement the former proved to be, in relation to our collection, extreme in type, the *rubra* having large spines for its head-width (which was large), and the *laevinodis* small spines for its head-width (which was small). The intermediates fell in the *laevinodis* group. We also sent Mr. Donisthorpe samples of the nests marked with circles in

[1] Santschi (1931) has maintained that Linnaeus was describing *M. ruginodis* Nyl. when he formed the species *M. rubra* L., and that the latter name has precedence. Santschi's nomenclature is used in this paper.

[2] Mean head-width (y) regresses on mean weight (x): for *rubra*, $y = \cdot 0840x + \cdot 8301$ where the standard error of the regression coefficient $= \cdot 0245$ millimetres per milligram.

[3] We wish to acknowledge the help which Mr. Donisthorpe kindly gave by both lending specimens from his collection and examining a number of our own.

fig. 2. These he said would fall into Forel's category but were "nearer *rubra*." Reasonable care has thus been taken to make the study as comprehensive as possible.

Compared with the measurement method of discrimination, the use of the rugosity character was inferior, partly because of the difficulty of making a clear distinction between wrinkled and smooth, and also because of the lack of consistence between the two methods. The workers from each of 22 nests assigned to the group *rubra* by measurement criteria were examined; of

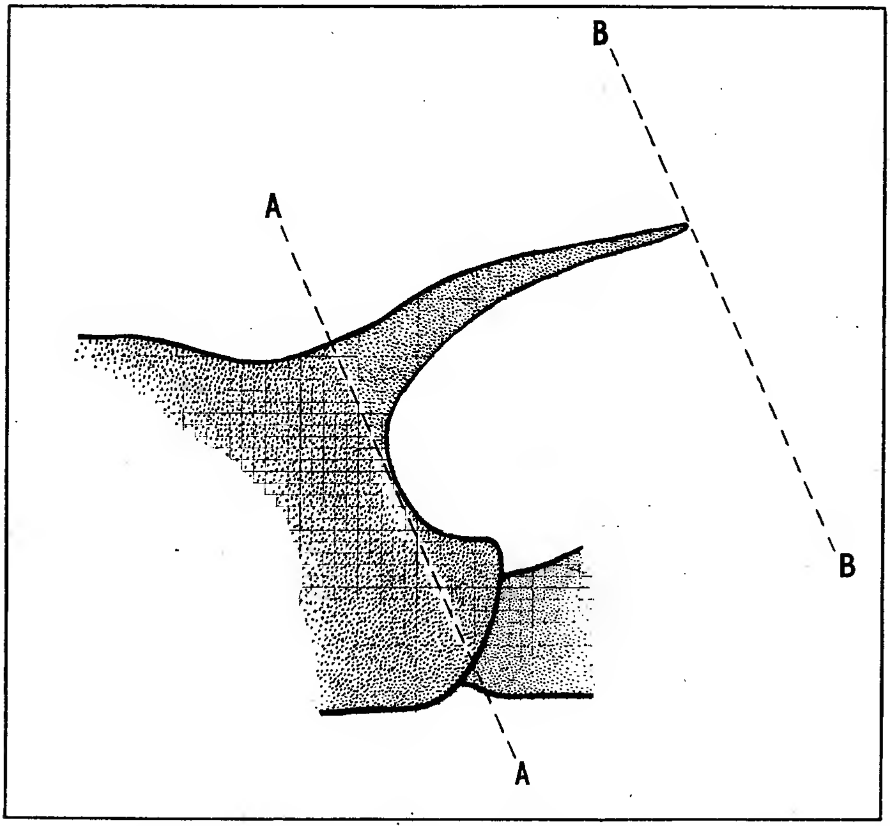

Fig. 1.—Spine of *M. rubra* ☿ from left side measured from A to B.

these 7 nests contained some workers with the area between the epinotal spines smooth (Table III), but these individuals did not have especially short spines. One nest which fell well within the *rubra* group (head-width 34 divisions = 1·030 mm., spine-length 27·6 divisions = ·380 mm.) had a majority of smooth workers in the sample. The position in *laevinodis* was less variable: of 180 workers from 18 nests, only 4 from 3 nests showed any sign of wrinkles. These were all of moderate spine-length, but many with larger spines were quite smooth. Thus in neither species did the character show any relation to spine-length. Nevertheless, discrimination by this method would in most cases

agree with the measurement method in distinguishing colonies with all or a majority of workers rugose (*rubra*) from colonies with all or a majority of their workers smooth (*laevinodis*), and it has one point in its favour—it can be used in the field with a hand lens.

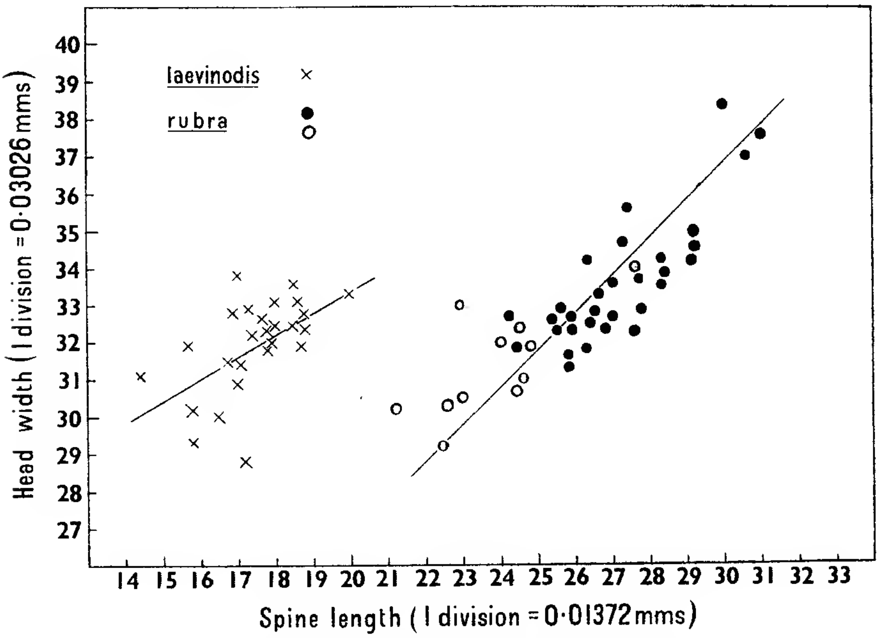

FIG. 2.—Relation of average worker head-width and spine-length in colonies of *M. laevinodis* and *M. rubra* showing regression lines.

TABLE I.—*Average Head-width and Average Spine-length in Millimetres, for Samples of* 25 *Workers from each of* 26 laevinodis *and* 42 rubra *Colonies Taken in Various Parts of the British Isles.*

	laevinodis.	*rubra.*
Mean head-width (x)	0·9665	0·9989
„ spine-length (y)	0·2397	0·3611
Correlation coefficients	0·8093 (< 1% P)	0·8528 (< 1% P)
Regression equations	$y = \cdot 2489x - \cdot 0009$	$y = \cdot 4593x - \cdot 0977$
S.E. of regression coefficients	0·03687	0·04449

Localities :

laevinodis :	3	colonies from	Glen Falloch, Perthshire.
	6	„ „	Ings, Westmorland.
	4	„ „	Great Barrow, Cheshire.
	3	„ „	Earlswood, Warwickshire.
	10	„ „	Harpenden, Hertfordshire.
rubra :	3	colonies from	Glen Falloch, Perthshire.
	26	„ „	Colgrain, Dumbartonshire.
	8	„ „	Ings, Westmorland.
	3	„ „	Delamere Forest, Cheshire.
	2	„ „	Harpenden, Hertfordshire.

Table II.—*The Frequencies of each Head-width, Spine-length Combination in* 1025 *Workers of* rubra (*from* 41 *colonies*) *and* 650 *Workers of* laevinodis (*from* 26 *Colonies*), *considered without regard to Colony Relationship. The data are grouped according to micrometer divisions: for head-width,* 1 *division* = ·03026 *mm.; for spine-length,* 1 *division* = ·01372 *mm.;* laevinodis *in italics.*

Spine-lengths.	Head-width.															
	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.	36.	37.	38.	39.	40.	41.
11	.	.	*1*	.	.	.	.	.	.	.	.	.	.	.	.	.
12	*1*	.	.	*2*	*2*	.	.	.	.	.	.	.	.	.	.	.
13	.	.	.	*5*	*4*	*1*	*6*	.	.	.	.	.	.	.	.	.
14	*1*	*3*	*1*	*6*	*1*	*9*	*3*	*3*	*1*	.	.	.	.	.	.	.
15	.	.	*5*	*10*	*8*	*10*	*13*	*7*	*2*	.	.	.	.	.	.	.
16	.	*3*	*2*	*6*	*9*	*26*	*19*	*16*	*9*	*1*	*2*	.	.	.	.	.
17	.	.	*7*	*5*	*16*	*19*	*49*	*22*	*17*	*3*	*2*	.	.	.	.	.
	1	.	1													
18	.	.	*1*	*6*	*12*	*16*	*25*	*25*	*10*	*3*	*2*	*1*	.	.	.	.
	1				1											
19	.	.	*3*	*3*	*6*	*11*	*15*	*18*	*19*	*4*	*1*	*1*	.	.	.	.
						1										
20	.	.	*1*	.	*4*	*14*	*20*	*15*	*13*	*8*	*1*	*1*	.	.	.	.
				2	1	1	1	1								
21	.	.	.	.	*2*	*1*	*7*	*7*	*9*	*4*	*2*	.	.	.	.	.
			2	6	8	10	7	7								
22	.	.	.	.	.	*1*	*3*	*1*	*4*	*2*	.	.	.	.	.	.
		1	3	6	8	10	7	5	1	.	1					
23	.	.	.	*1*	.	.	.	*1*	*1*	*3*	.	.	.	.	.	.
				7	11	16	15	9	2	1						
24	.	.	.	.	.	.	.	*2*	.	.	*1*	*1*	.	.	.	.
			2	1	7	12	19	9	7	1						
25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
				3	8	22	28	25	10	6	1					
26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
					4	17	29	49	26	15	1	1				
27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
					3	10	42	33	45	17	9	1	2	1		
28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
					1	3	10	25	38	17	8	5	.	1		
29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
					1	1	10	11	28	22	12	9	4	2		
30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
						2	4	10	15	31	12	7	4	2	1	
31	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
								5	6	10	17	5	11	1	.	1
32	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
									3	5	6	8	6	.	1	
33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
										1	4	3	2	3		
34	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
										1	2	.	2	1		
35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
											1	1	.	.	1	
36	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
													1	.	.	1

It will be noticed that mean head-size did not differ very much, but that mean spine-length did ; also that the slope of the *rubra* line was greater than that of *laevinodis*, but the significance of this is not clear.

Although the regression groups remain reasonably discrete when based on colony means, they intermingle slightly when individual workers are considered. The extent of this may be seen from Table II.

TABLE III.—*Showing the Frequency with which a Sample of* 10 *Workers from each of* 22 rubra *and* 18 laevinodis *Colonies Contained* 0 *to* 10 *Specimens having the Area between the Epinotal Spines Smooth.*

Number with smooth area.	*rubra.*	*laevinodis.*
10	—	15
9	—	2
8	—	1
7	1*	—
6	—	—
5	—	—
4	—	—
3	1	—
2	2	—
1	3	—
0	15	—
	22	18

* By dimensions this was clearly a *rubra* colony (head-width, 34 divisions = 1·030 mm., spine-length 27·6 divisions = ·380 mm.).

Other differences between the two species are more conveniently mentioned in the third section of this paper.

2. VARIATION WITHIN *M. rubra* L.

Suspicions that the species *rubra* was heterogeneous were aroused in the early stages of experimental sociological studies. These were later confirmed, and it was found that there existed two forms, each self-propagating, which may be briefly contrasted and named as follows :

var. **macrogyna** var. nov.: females and males larger, colonies usually monogynous with relatively large aggressive workers, the average worker head-width less than the average female head-width, colony reproduction by dissemination of fertile females which found colonies either alone or in small aggregates ;

var. **microgyna** var. nov.: females and males smaller, colonies polygynous with relatively small and docile workers, the average worker head-width similar to the average female head-width, fertile females return to their nest (and possibly other nests) and colonies reproduce by fission.

The two forms are not sharply distinct, but intermediates are rare in comparison with the types. The evidence for these statements will now be presented.

(a) *Head-width Measurements of Queens.*

Colonies were collected, the queens (deälate females) removed and counted and the width of their heads measured. The results are set out in Table IV and illustrated in fig. 3.

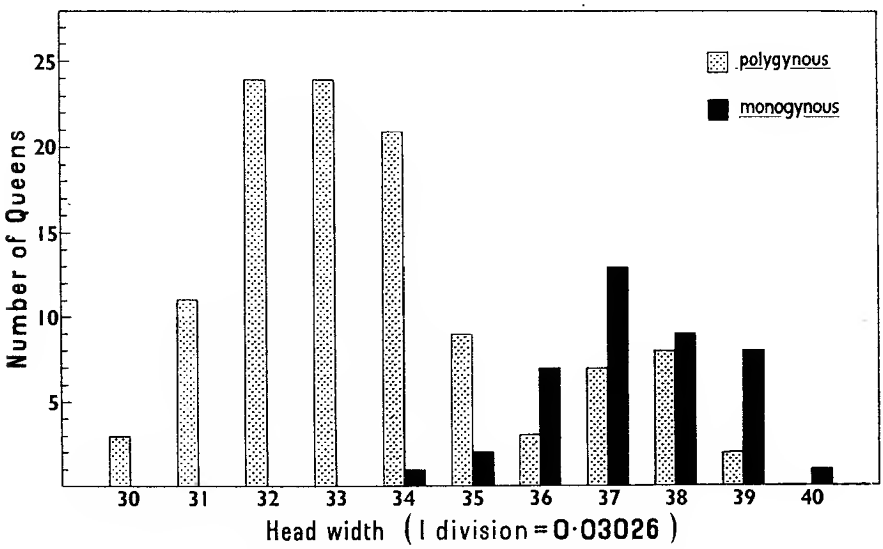

Fig. 3.—Head-width distribution of queens from polygynous and monogynous colonies of *M. rubra.*

Table IV.—*Head-width Frequencies of Queens in* 23 *Polygynous* (2–15 *Queens per Nest*) *and* 41 *Monogynous Colonies of* M. rubra. *Head-widths in micrometer divisions* (1 *division* = ·03026 *mm.*)

	Head-width.											Total.
	30.	31.	32.	33.	34	35.	36.	37.	38.	39.	40.	
Polygynous	3	11	24	24	21	9	3	7	8	2	.	112
Monogynous	.	.	.	.	1	2	7	13	9	8	1	41
Total	3	11	24	24	22	11	10	20	17	10	1	153

A tendency towards an association of monogyny with macrogyny, and polygyny with microgyny[4] is apparent. The combined results from the 64 nests show a bimodal frequency distribution, the medium head-widths being rarer than either larger or smaller ones.

The slight rise in frequency of the larger head sizes in polygynous nests is at first difficult to interpret. We believe it to be caused by the fact that *macrogyna* queens sometimes associate in colony-founding (primary pleometrose, Wasmann, 1910) and do not separate when workers are produced (as happens, for example, in *Lasius niger* Linn.), but it is possible that an alternative explanation, that queens may sometimes gain access to nests which already

[4] The small queens, as will be shown later, have workers whose average head-width is slightly larger than their own, so that they are properly called microgynes in the conventional sense of that word, being females as small as or smaller than their workers.

possess one (secondary pleometrose), may supplement the first. Our contention is supported by two lines of evidence: first, that groups of freshly fecundated *macrogyna* queens set together in observation nests lived and reared workers amicably, and secondly, that quite a close parallel exists between the frequencies with which groups of 1, 2, 3, 4, etc., queens are found in process of colony-founding and the frequencies with which these numbers of queens are associated in mature colonies (Table V).

Table V.—*An Analysis of* 35 *Colony-founding Groups of Queens to Show Head-width* (1 *division* = ·03026 *mm.*) *and Group-size Frequencies. For Comparison, Queen Group-size Frequencies in* 43 *Mature* macrogyna* *Colonies are given.*

Size of Group.	Head-widths.								Number of groups.	Number of mature nests with 1, 2, 3, etc., queens.
	33.	34.	35.	36.	37.	38.	39.	40.		
1 ♀	.	1	1	7	9	5	6	1	30	38
2	.	.	.	1	2	1	2	.	3	1
3	.	.	.	.	.	.	.	.	0	2
4	.	.	.	.	2	1	.	1	1	1
5	.	.	.	.	.	.	.	.	0	0
6	1	2	1	1	1	.	.	.	1	1
	1	3	2	9	14	7	8	2	35	43

* That is, where all queens present, if more than one, exceeded 36 divisions in head-width.

Since very few *microgyna* females were discovered in autumn in process of founding colonies, it was reasonable to suppose that their normal habit was to return to mature nests of their own type. This was confirmed by examination of queens in *microgyna* nests in autumn. Dissection showed that they fell into two categories, one having ovaries with well developed yolky oocytes and terminal *corpora lutea*—the old laying queens—and the other having moderately yolky oocytes but no *corpora lutea*—the young queens added since the nuptials, whose ovaries had developed a little, but not ovulated.[5]

Further confirmation of these results was obtained experimentally.

(b) *Experimental Introduction of Queens.*

Recently fecundated females of a range of head-sizes were added to queenless colonies of both *macrogyna* and *microgyna* types in observation nests and the reactions noted. Six colonies, three of each type were used, each consisting of about 50 workers and brood. Six queens, of each head-width from 34 to 39 divisions, were added three at a time to each nest. Reactions were usually definite, and it was not necessary to leave the queens in for more than a few minutes. Either they were attacked immediately by workers with opened mandibles, and dragged about relentlessly, or they were quickly examined, given food, and allowed to brood. But in certain cases, a worker, on approaching an introduced queen, opened its mandibles without attacking,

[5] It is usual in *M. rubra macrogyna* for young queens to begin laying in the spring following nuptials (in contrast to *Lasius niger* and *L. flavus*), but on one occasion we have found a group of queens with a single egg.

and after a pause, went away. This we have described as "menacing," but we think it probably results from an interaction between the intensity of stimulation and the constitutional peculiarities of the subject, being evoked by normal stimulation of a constitutionally unaggressive worker, or under-stimulation of a constitutionally normal worker. These results are set out in Table VI.

TABLE VI.—*Queen Introduction Experiments: 6 Early Post-nuptial Females of each Head-size were Added in Two Separate Groups of 3, to each of 3* macrogyna *and* 3 microgyna *Groups of Workers and Brood. In each column of the Table, Numbers Tolerated, Menaced, and Attacked, are set out so: T, M, A.*

Head-width of female.	Three *macrogyna* groups.			Three *microgyna* groups.		
	1.	2.	3.	1.	2.	3.
39 and over	4–1–1	3–0–3	3–1–2	0–0–6	0–1–5	0–0–6
38	1–2–3	0–2–4	1–2–3	0–0–6	0–0–6	0–2–4
37	3–3–0	0–2–4	4–2–0	0–0–6	0–0–6	0–3–3
36	3–0–3	0–0–6	1–1–4	2–2–2	3–0–3	2–2–2
35	0–0–6	0–0–6	0–0–6	6–0–0	6–0–0	6–0–0
34 and less	0–0–6	0–0–6	0–1–5	6–0–0	6–0–0	6–0–0

These results very clearly confirm the existence of two varieties. We may note the following points:

(1) Groups of workers within each type differed slightly in their reactions. Thus *macrogyna* 2 were relatively aggressive, whilst *microgyna* 3 were relatively tolerant.

(2) All *macrogyna* rejected queens of 35 and less divisions whereas all *microgyna* accepted them.

(3) *Microgyna* attacked all queens of greater head-width than 36 divisions, but *macrogyna*, instead of accepting them as might at first be expected, rejected sometimes and accepted at other times. Perhaps this is due to an unnatural circumstance, for we have good reason to suppose that large queens do not usually attempt to re-enter mature colonies.

(4) Intermediate behaviour was shown towards queens of head-width 36 divisions by all groups except group 2 *macrogyna* which was an aggressive type. This may indicate that the change in ant-perceptible character[6] takes place gradually within the head-size 36, and that a queen of this size only evokes aggressive behaviour in hostilely disposed workers.

(5) On the other hand, the narrowness of the transition belt is surprising, and the possibility that two types are included in the size 36 cannot be dismissed. This was the subject of a further experiment reported in a later section.

(c) *Experimental Mixing of Workers.*

Workers of like and unlike varieties were mixed on a number of occasions using each time 10 of each. After 2 minutes the number fighting was recorded. These results are summarized in Table VII.

[6] Observations indicate that perception is made without contact, at a distance of a few millimetres, thus indicating an olfactory mechanism.

TABLE VII.—*Workers of the Two Varieties* microgyna *and* macrogyna *were Mixed: 10 of Each Type (but from different Colonies) were used, and the Number Fighting after 2 Minutes Recorded. Below are Shown the Proportion of Cases in which No Fighting Took Place.*

	Macrogyna with *macrogyna.*	*Macrogyna* with *microgyna.*	*Microgyna* with *microgyna.*
Number of tests	16	19	19
„ with no fighting	4	1	15

They clearly indicate that mixing of dissimilar types gives the greatest chance of antagonism.[7] But, whereas mixtures of *microgyna* workers were usually peaceful, mixtures of *macrogyna* usually resulted in combat. In this respect, striking consonance was shown with the results of introducing queens. Thus, the *macrogyna* were frequently intolerant of both queens and workers of their own type. It is possible that the underlying cause may prove to be due to the existence of genetically differing strains, each type passed from queen to worker progeny, but it is also quite likely that the preponderance of antagonistic reactions is the result of living in separate isolated colonies derived from single queens. The *microgyna*, habituated to rather diverse associates in their polygynous nests, were as a rule tolerant of queens and workers of their own variety, but strongly intolerant of those of the other kind.

(d) *Special Consideration of Intermediates.*

As some of the principal characters of the two varieties have been contrasted, it is important now to consider the intermediates.

Queens of Head-width 36 Divisions (= 1·090 mm.).

Queens of this head-size have been found behaving as *macrogyna* more often than as *microgyna*. As *macrogyna* we have the following cases: 7 specimens were the sole queens in nests, and 1 specimen was associated with two larger queens in a 3-queen *macrogyna* nest (Table IV); 7 queens have been found alone and 1 with a larger queen presumably colony-founding (Table V); 1 queen was found in a 6-queen aggregate of which 1 was larger and 4 were smaller (Table V). Of queens behaving as *microgyna* we have only 2 specimens associated with smaller queens in polygynous colonies (part of Table IV).

In queen introduction experiments (Table VI) it was noted that *microgyna* workers rejected a large proportion of these queens, and *macrogyna* workers accepted a few. Worker reaction to this head-size was specially investigated,

[7] Statistical analysis might proceed as follows:

(1) Comparison of column 2 with column 3: 16 cases of no fighting would be expected divided evenly between the two groups if no bias, $\chi^2 = 12\cdot25$, < 1 per cent. *P.*

(2) Comparison of column 1 with column 3: 19 cases of no fighting would divide in the ratio 19/16 if no bias, $\chi^2 = 4\cdot66$, 1–5 per cent. *P.*

(3) Comparison of column 1 with column 2: 5 cases of no fighting would divide in the ratio 16/19 if no bias, $\chi^2 = 2\cdot36$, 10–20 per cent. *P.*

using the same 6 nests as before (3 of each variety). Fourteen queens were introduced separately giving a total of 42 test reactions for each *rubra* type (Table VIII).

TABLE VIII.—*The Reactions of* 3 microgyna *and* 3 macrogyna *Groups of Workers and Brood to* 14 *Queens of Head-width* 36 *Divisions* (= 1·090 *mm.*) *were Tested by Adding each Queen Separately: T = tolerated, M = menaced, A = attacked.*

Queen number.	Three *microgyna* groups. 1,	2,	3,	Three *macrogyna* groups. 1,	2,	3,
4	T	T	T	T	A	A
8	T	M	T	A	A	A
6	M	T	M	A	A	A
1	M	A	M	T	A	M
11	M	A	M	M	M	T
9	A	M	A	M	M	M
10	A	A	M	T	T	M
12	A	A	M	M	M	A
2	A	A	A	T	T	T
3	A	A	A	T	A	T
13	A	A	A	T	M	A
14	A	A	A	A	M	A
5	A	A	A	A	M	A
7	A	A	A	T	M	M

It will be noticed that no queen which was tolerated by one group of *microgyna* was attacked by another group. Menacing appears as an intermediate form of behaviour, and it is possible to arrange the queens in a series from those unanimously tolerated to those unanimously attacked, as has been done in the table. When this is done on a basis of reactions by *microgyna*, a certain order appears in the, at first sight, chaotic reactions of the *macrogyna* groups; the first three queens, which may be described as "tending to be tolerated" by the *microgyna*, are seen to be very much more consistently attacked than the others. These results thus come into line with earlier ones in which a wider range of head-size was used, and, in fact it is evidence that within this single head-width group a gradual transition from *microgyna* to *macrogyna* occurs, and that it contains more of the latter type.

Since queens exist towards which reaction is intermediate, we may reasonably regard this as strong evidence that the *rubra* species is composed of two forms connected by transition types, rather than by two forms distinct in ant-recognizable characters, but of overlapping head-widths.

Queens of head-width 35 *divisions* (= 1·060 *mm.*).

Most of the queens in this class behaved as *microgyna*. We have the following cases: 9 specimens were associated with smaller queens in polygynous colonies (Table IV). Queens behaving as *macrogyna* were as follows: 2 specimens were the sole queens in mature colonies (Table IV), 1 specimen was found alone, and 1 in the aggregate of 6 queens already referred to (Table V), which were presumed to be founding colonies. In queen introduction experiments (Table VI), they were consistently accepted by *microgyna*, and rejected by *macrogyna*.

(e) *Exceptional Cases: Atypical Behaviour.*

A few exceptional cases should be noted. One queen of head-width 33 divisions was discovered in a colony-founding aggregate (Table V), whereas in 24 other cases of the same size queens were in polygynous colonies of *microgyna*. In this same curious aggregate there were 2 queens size 34 divisions, and another queen of this size has been discovered alone, but in 21 other cases they have been queens in colonies with smaller queens. One large queen (head-width 37 divisions) was collected with 3 definitely *microgyna* queens in a mature colony, whereas in 19 other cases this size have been either alone or with larger queens in fully developed colonies.

(f) *The Relation between Head-widths of Queens and Winged Females in the Same Nest.*

The measurements to be described indicated that each variety tended to be self-propagating, though (if head-width criteria are to be trusted) cases were found where both types arose from a single queen.

In 10 colonies of *macrogyna* examined, a close correlation existed between the head-width of the queen and the average of 25 virgins ($r = +\cdot 9126$, < 1 per cent. P). The equation of the linear regression was $y = \cdot 9302x + \cdot 081$, where y is the average virgin head-width, and x the head-width of the queen, both measured in millimetres (S.E. of regression coefficient $= \cdot 1473$ mm.). The average head-width of queens, 1·117 mm., differed little from the average for all virgins, 1·120 mm. The frequency distributions of the virgin head-widths are shown in Table IX.

TABLE IX.—*Frequency Distributions of Female Head-widths in Micrometer Divisions (1 division = ·03026 mm.), from* 10 macrogyna *Colonies.*

Head-width.	Colony number.									
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
33	6	.	.	.	.	.	.	.	.	.
34	5	.	.	.	.	.	.	.	.	.
35	10*	5	1	4	.	1	.	.	.	.
36	4	16*	12*	11*	4	2	1	.	.	.
37	.	4	12	8	3*	5*	16*	5	.	5
38	.	.	.	2	3	13	8	17*	9*	12
39	.	.	.	.	.	4	.	3	10	8*
40	.	.	.	.	.	.	.	.	1	.
41	.	.	.	.	.	.	.	.	1	.

* Head-width of queen.

It will be noted that dispersion was usually small. Also that in 3 cases out of 10 the queen's size was not the modal one, and in 4 of the 7 cases where it was, the distribution was asymmetrical. We may, perhaps, look to the unknown male parent or parents for the explanation of this.

With *microgyna*, no correlation was obtained between the average head-widths of virgins and of queens from the same nest. This is not surprising, in view of the heterogeneity of queen head-size in each nest. But it is probable that a similar relation exists for small as for large queens (see, for example, the instance of colony 1 in Table IX). The frequency distributions of virgin

head-width are shown in Table X, that of the queens being included as well. In colony 1 it would seem likely that only one queen has been instrumental in forming female progeny. The average head-widths of queens, 0·995 mm., was similar to that of virgins, 0·985 mm.

TABLE X.—*Frequency Distributions of Virgin Female (V) and Queen (Q). Head-widths in* 6 microgyna *Colonies, in Micrometer Divisions,* (1 *division* = ·03026 *mm.*)

Head-width.	Nest numbers. 1.		2.		3.		4.		5.		6.	
	V.	Q.	V.	Q.	V.	Q.	V.	Q.	V.	Q.	V.	Q.
30	5	.	.	.	1	.	.	.	.	.	.	.
31	9	1	2	1	4	1	1	.	.	.	.	.
32	2	.	11	1	10	1	6	2	5	4	2	.
33	.	3	4	1	8	1	8	3	14	3	5	.
34	.	2	.	.	2	.	1	.	5	1	11	1
35	.	.	.	.	.	.	.	.	1	.	7	1
36	.	1	.	.	.	.	.	.	.	.	.	.

(g) *The Relation between Head-widths of Queens and Workers in the Same Nest.*

Macrogyna showed a good correlation between queen and average worker head-widths ($r = +\cdot 6740$, < 1 per cent. P). The workers were on the average smaller than their queens, averaging 1·069 mm. (= 35·34 divisions) as opposed to 1·113 mm. (= 36·78 divisions). The regression equation was $y = \cdot 817\,x + \cdot 160$, where y is the expected average head-width of workers, and x the actual head-width of the queen, both in millimetres (S.E. of regression coefficient = ·0258 mm.). The variation of worker size in each colony was greater than that of virgins (Table XI).

TABLE XI.—*Frequency Distributions of Worker Head-widths in* 10 *Colonies of* macrogyna, *in Micrometer Divisions* (1 *division* = ·03026 *mm.*).

Head-width.	Nest number. 1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
30	1	.	.	.	.	.	.	.	.	.
31	4	.	.	.	.	.	.	.	.	.
32	14	1	2	.	1	.	.	.	.	.
33	15	5	8	3	5	.	1	.	.	1
34	9	5	8	9	12	2	.	2	.	.
35	3*	11	7	14	17	5	5	8	.	2
36	4	2*	*	15	12	14	12	8	5	4
37	.	.	.	8*	3*	14*	5*	7	8	1
38	.	1	.	1	.	12	2	*	8*	12
39	.	.	.	.	.	3	.	.	4	5*

* Head-width of queen.

For *microgyna*, no correlation could be detected between mean worker and mean queen head-width. The workers were on the whole smaller than those of *macrogyna*. They averaged 1·005 mm. (= 33·2 divisions), and were thus just a little larger than their queens, which averaged 0·995 mm. (=32·9

divisions). In this respect they contrast with *macrogyna*, and are microgynes in the conventional sense of the word.[8] The frequency distributions of head-width for workers and queens from 10 colonies are shown in Table XII .

TABLE XII.—*Head-width Frequencies in Workers (W) and Queens (Q) from 10 Colonies of* microgyna, *in Micrometer Divisions* (1 *division* = ·03026 *mm.*).

Head-width.	Number of colony. 1.		2.		3.		4.		5.		6.		7.		8.		9.		10.	
	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.
28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
29	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.
30	.	.	.	.	.	.	2	.	1	.	1	1	.	.	.	.	.	.	4	.
31	1	.	.	.	4	.	1	1	6	.	3	2	1	.	2	.	2	.	5	4
32	8	4	1	.	4	.	4	1	3	2	6	5	1	1	8	4	6	1	6	2
33	5	3	.	.	12	3	11	1	7	3	12	4	1	3	9	.	8	.	4	1
34	8	1	3	1	4	2	6	.	3	.	3	2	11	1	4	.	6	.	.	.
35	1	.	7	1	.	.	.	.	2	.	.	.	7	.	1	.	3	1	.	.
36	.	.	10	.	1	1	1	.	3	.	.	.	3	.	1	.	.	1	1	.
37	1	.	3	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
38	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

(h) *The Head-widths of Males.*

Microgyna males averaged less than *macrogyna* males, ·910 mm. (= 30·12 divisions) instead of ·980 mm. (= 32·42 divisions), but the difference was so small compared with the variability that the frequency distributions overlapped (Table XIII), and when combined gave little sign of bimodality, as did the female distributions. The total male range of size was less than the female range, 8 divisions (·2421 mm.) instead of 10 divisions (·3026 mm.).

TABLE XIII.—*Head-width Frequency Distributions of Males from* 5 macrogyna *and* 5 microgyna *Colonies in Micrometer Divisions* (1 *division* = ·03026 *mm.*).

Head-width.	Five *microgyna* colonies. 1.	2.	3.	4.	5.	Five *macrogyna* colonies. 1.	2.	3.	4.	5.	Total.
27	1	.	.	.	.	.	.	.	.	.	1
28	5	2	.	.	.	1	.	.	.	.	8
29	12	9	2	1	1	2	.	.	.	.	27
30	6	10	3	6	9	6	3	.	.	.	43
31	1	4	5	10	11	8	7	2	.	.	48
32	.	.	3	3	3	4	10	7	1	6	37
33	.	.	1	1	.	4	5	14	8	12	45
34	.	.	.	.	.	.	.	2	12	6	20
35	.	.	.	.	.	.	.	.	4	1	5

As it had already been found that virgins and queens tended to have similar head-widths in each colony, the male data were related to virgin data. This was more easily done and did not involve destruction of the queen or queens. Taking both varieties together a good positive correlation was

[8] But it should be noted that there is not a fundamental difference here, for the regression relating *macrogyna* queens and workers, if extrapolated towards the origin, passes into a region where queens are smaller than their worker progeny.

obtained ($r = +\cdot 8150$, < 1 per cent. P), giving a regression equation of $y = \cdot 4764x + \cdot 445$, y being the expected average male head-width, and x the average virgin head-width. Males as a group had narrower heads than virgins.

(i) *Two Morphological Trends in Queens.*

The largest queens of *macrogyna* (head-widths 39 and 40 divisions) had the dorsal part of their heads dark brown to black in colour: this merged rapidly into orange-brown below at a line level with the eyes. The smallest queens of *microgyna* were less dark on the head, and this changed more gradually to a yellow rather than an orange-brown below. In general, the lighter parts of the bodies of the largest queens were orange-brown and this made the former appear contrasting black and orange and the latter a more uniform dull brown. But no sharp distinction was possible, for a trend closely associated with head-width joined one extreme to the other.

A similar trend in form of ovary was observed: the ovarioles in virgin *microgyna* were typically only two-thirds their length in *macrogyna*. In form they differed as follows: the terminal filament in the largest queens occupied one-third of the length, but in the smallest queens two-fifths, so that the major difference in total ovariole length was due to germarium size. The ovarioles also differed in shape: in *microgyna* they were typically twice as wide in the terminal filament end and only half as wide at the oviduct end as in large *macrogyna* queens. Such differences are probably associated with a smaller fecundity in *microgyna*, which is no doubt compensated by the number of queens in their colonies.

One further anatomical point was noticed: the eyes of queens of both types were approximately the same size, and this made them appear more prominent in the smaller ones.

(j) *Distribution.*

We have found both varieties of *rubra* at Colgrain, Dumbartonshire, and also in Glen Falloch, Perthshire, 25 miles to the north. We have found *microgyna* at Ings, Westmorland, and at Great Barrow, Cheshire.

Certain remarks in the literature make it probable that both varieties have a wide distribution. Thus Donisthorpe (1927, p. 129) states:

> "On April 30th, 1912, I found three small females, partly winged, under a stone, in a colony of *ruginodis* at Hynish, in the Isle of Tiree. S. O. Taylor captured a winged *microgyne* of this species at Wakerley Wood, Northamptonshire, on August 17th, 1915. Wasmann took a number of winged females in a nest of *ruginodis* at Vorarlberg, Feldkirch, in August, 1890, which were smaller than the workers of the same colony."

And later, whilst discussing a colony of *M. laevinodis* var. *ruginodo-laevinodis* Forel found on Lundy Island (*loc. cit.*, p. 124) he says:

> "A small deälated female found in this colony only measures 5·5 mm."

Perhaps a great many colonies of *microgyna* have in the past been relegated to Forel's intermediate category.

3. Further Observations on *Myrmica laevinodis* Nylander.

Measurement of 192 queen *laevinodis* from 22 colonies collected from Herts, Cheshire and Perthshire gave no evidence of polymorphism. The frequency distribution (Table 14) was symmetrical and unimodal.

Table XIV.—*Head-width Frequencies of Queens and Workers of* M. laevinodis *in Micrometer Divisions (1 division* = ·03026 *mm.).*

	Head-widths.															Total.
	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.	36.	37.	38.	39.	40.	
Queens	.	.	.	.	.	.	.	.	.	9	29	63	57	28	6	192
Workers	2	6	21	44	64	107	158	116	85	28	11	4	.	.	.	646

Mean head-widths : Queens, 37·27 divisions = 1·1278 mm.
Workers, 32·11 „ = 0·9716 „

The mean head-width was very near that of *M. rubra* var. *macrogyna*, 1·1278 mm. (= 37·27 divisions) as compared with 1·1130 mm. (= 36·78 divisions), but the workers averaged smaller, 0·9716 mm. (= 32·11 divisions) as opposed to 1·069 mm. (= 35·34 divisions). They were, in fact, comparable to *microgyna* workers, 1·005 mm. (= 33·2 divisions).

The correlation between the average head-widths of workers, taking a sample of 25 from each of 17 colonies, and the average for queens from the same nest was not very good ($r = +\cdot 4976$, $P = 1$–5 per cent.), but the following regression equation was obtained : $y = \cdot 3531x + \cdot 5734$, where y is the average worker head-width, and x the average queen head-width in millimetres. The poorness of this correlation is no doubt due to the fact that most of the colonies were polygynous, and some had over 100 queens.

The frequency distributions of worker head-sizes for 10 randomly selected colonies is shown in Table XV.

Table XV.—*Frequency Distributions of Worker Head-widths from* 10 *Colonies of* laevinodis, *in Micrometer Divisions* (1 *division* = ·03026 *mm.*).

Head-widths.	Colony number.									
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
26	.	.	.	.	.	2	.	.	.	.
27	.	.	.	2	.	3	.	.	.	.
28	.	1	.	5	.	8	1	1	.	.
29	1	7	1	7	2	3	.	1	.	1
30	3	6	.	6	7	4	3	2	.	3
31	2	8	6	4	6	5	6	.	4	5
32	9	2	9	1	9	.	5	7	12	6
33	3	1	2	.	1	.	6	5	6	5
34	5	.	4	.	.	.	4	6	3	3
35	2	.	2	.	.	.	.	1	.	2
36	.	.	1	.	.	.	.	.	.	.
37	.	.	.	.	.	.	.	2	.	.

The variability is comparable with that of both types of *rubra*. In aggregate this data forms a symmetrical unimodal frequency distribution (see

Table XIV)[9]. *Laevinodis* thus appears to combine in a single form—the macrogyne—characters which, in *rubra*, are divided between two forms.

4. Discussion.

In this paper we have presented evidence to show that *rubra* is an incompletely dimorphic species. A case in plants which is perhaps analogous, has been described: the Lesser Celandine (*Ranunculus ficaria* Linn.) occurs in two forms, one setting viable seed and the other reproducing vegetatively by means of tubercles (Marsden-Jones, 1935; Metcalfe, 1938 and 1939). In ants, Gösswald (1942) has shown that *Formica rufa* L. consists of several races, some of which differ in ways similar to those just described in *Myrmica rubra*. *F. rufa rufa* is equivalent to *M. rubra* var. *macrogyna*, as it has monogynous colonies, and queens with long ovarioles which lay many eggs; the queens found colonies by entering nests of *Formica fusca* L. *F. rufa rufo-pratensis minor* is equivalent to *M. rubra* var. *microgyna*, for it exists in polygynous, polydomous colonies, and has queens that are relatively small (though not as small as their workers), with short ovarioles and low fecundity. *F. rufa rufo-pratensis major* has intermediate characters. Talbot (1948), has recently found that two varieties of another species of *Formica* differ, amongst other ways, in whether they are monogynous or polygynous. *Formica pallidefulva nitidiventris* Emery was monogynous in all of 24 nests examined and recorded, whereas *F. pallidefulva schaufussi incerta* Emery was frequently polygynous, and Talbot suggests that secondary pleometrose and colony fission occurred. In this case microgyny was not involved, but Holliday (1903) has recorded microgynes of the former variety.

In the area from which our colonies of *M. rubra* have been collected, *macrogyna* has predominated in transitory habitats, and those which have only been suitable for ant colonization for a short time (e.g. in seral and mosaic cyclic vegetation types) whereas *microgyna* has been found in comparatively stable areas. Gösswald lists a wider range of habitat occurrences for the monogynous form of *F. rufa*. than for the polygynous form, and comments that the latter lives in especially favourable ant sites. In both these cases two possibilities appear to exist: either that the polygynous form is gradually derived from the monogynous in each habitat that persists for long enough in a favourable condition, or that each species is developing (or has developed), in an evolutionary sense, varieties adapted to temporary and stable habitats respectively; hybridization of these may still occur. Such problems are being investigated.

Wheeler (1937) has reviewed the subject of microgynes, and pointed out that these females occur as "occasional anomalies," or "complemental females," in a wide variety of ants. Donisthorpe (1927, p. 122) recorded an instance of a microgyne *laevinodis*, which was sole queen in a nest, and Reichensperger (1911) has recorded two similar cases in *Plagiolepis pygmaea* Latreille which he regarded as successfully established mutants. In the subgenus *Microgyna* of the genus *Formica* the only known females are microgynes. *M. rubra* appears to lie between these extremes.

[9] This is also the case with *rubra*, if workers of the two varieties are pooled and considered together.

5. Summary.

1. A biometrical study of the similar species, *Myrmica laevinodis* Nylander and *Myrmica rubra* L., has shown within the limits of the material available, that colonies of one species can be distinguished from colonies of the other, and that, as a result, Forel's intermediate category, *Myrmica laevinodis* var. *ruginodo-laevinodis,* will probably disappear. A certain number of individual workers of each species were indistinguishable.

2. *M. rubra* has been shown to exist in two varieties, occurring together in various localities, and both probably widespread, showing a gradual transition of morphological characters and a more abrupt transition of ant-perceptible characters. Each variety differs primarily in its propagation methods : the one having the primitive method of dissemination of fecundated queens which may found colonies alone or in aggregate ; the other, receiving queens after nuptials back into their nests, being highly polygynous as a result, and reproducing by fission of polydomous societies. The former variety is macrogynous, and the latter microgynous. New names are introduced for these varieties.

3. *M. laevinodis* gave no evidence of polymorphism, and appears to combine in a single form—the macrogyne—the characters divided between two forms of *rubra.*

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